



British Ecological Society

Stemwood Biomass and Production During Spruce-Fir Stand Development

Author(s): G. H. Aplet, F. W. Smith and R. D. Laven

Source: *Journal of Ecology*, Vol. 77, No. 1 (Mar., 1989), pp. 70-77

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/2260917>

Accessed: 14/11/2013 11:33

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Ecology*.

<http://www.jstor.org>

STEMWOOD BIOMASS AND PRODUCTION DURING SPRUCE–FIR STAND DEVELOPMENT

G. H. APLET, F. W. SMITH AND R. D. LAVEN

*Department of Forest and Wood Sciences, Colorado State University, Fort Collins,
Colorado 80523, U.S.A.*

SUMMARY

(1) A 600-year chronosequence of Engelmann spruce–subalpine fir forest was used to examine the effects of changes in forest structure on stemwood biomass and production in a mixed-species community.

(2) Fir size-class and age-class structure stabilized early in stand development, but spruce size and age structure changed throughout stand development.

(3) Community stemwood biomass remained nearly constant through time as an increase in spruce biomass compensated for mortality in the fir component.

(4) Fir production decreased from initially high levels with change in size-class structure, but spruce production remained nearly constant.

(5) Stemwood production was related to leaf area in both species, but patterns of leaf-area allocation differed between species.

(6) Constant fir leaf area and production are achieved after stand structure stabilizes, but constant spruce leaf area and production occurred despite changes in stand structure.

INTRODUCTION

Although biomass accumulation and net primary production are important components of vegetation change, a consensus on general patterns has not developed. Peet (1981a) discussed and unified three disparate descriptions of biomass accretion and net primary production in a model describing stand development in terms of time lags in regeneration and mortality. Where regeneration and mortality are continuous, biomass will rise to a steady state with time. Where mortality is episodic and occurs after some period of stand development, biomass will overshoot the steady state and then fall to an equilibrium level following overstorey mortality. If regeneration is excluded due to overstorey density, and mortality is abrupt, live biomass will fall below the expected equilibrium, and further stand development results in a series of damped oscillations around a steady state. Changes in net primary production are similarly related to regeneration and mortality in this model.

This unified model incorporates population processes into a representation of functional as well as structural community change. Previously, changes in biomass and production have been attributed to differences in species composition (Horn 1971, 1974), size structure (Margalef 1963; Odum 1969) or nutrient availability (Vitousek & Reiners 1975). Peet's model describes biomass and production change as a function of recruitment, growth and mortality. Support for this model is offered in the form of age sequences of biomass and net primary production levels from monospecific and mixed-species stands. However, the effects of individual species population dynamics on biomass and production in mixed-species communities are not included in Peet's explanation. A population of a shade-intolerant tree species, for example, may display periods when there is no recruitment and when mortality is expressed; this population then behaves

TABLE 1. Site description and ages for nine spruce–fir stands in north-central Colorado.

Stand	Age	Elevation (m)	Aspect	Slope°	Spruce age range	Fir age range
1	125	3250	N	5	50–125	75–125
2	175	3150	E	11	75–175	100–175
3	275	3250	NW	23	175–275	125–275
4	275	3250	N	15	175–275	100–275
5	375	2900	E	25	75–375	75–325
6	375	3150	NE	13	200–375	100–350
7	575	3200	NE	13	325–575	100–450
8	575	3150	NE	22	50–575	50–450
9	700	3150	NW	15	200–700	125–400

according to the third model of biomass dynamics. Another species which recruits continuously and dies over a broader range of ages may follow the first or second model. The predicted dynamics of a community composed of a combination of these two species is much less clear.

The objective of this paper is to address the effect of population dynamics on biomass and production in a two-species community. We analyse changes in stemwood biomass and production as indicators of total biomass and net primary production along a nine-stand chronosequence of an Engelmann spruce (*Picea engelmannii* (Parry) Engelm.)–subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest representing 600 years of stand development.

METHODS

Community description

This study was conducted in the Engelmann spruce–subalpine fir forests of the Cache La Poudre and Laramie River watersheds in north-central Colorado (40°30'N, 105°50'W). Here the spruce–fir forest occurs on all but southerly exposures above 2800 m between the lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) zone and the treeline (Peet 1981b). Spruce and fir share dominance in the overstorey. Fir is considered the better species at establishing in the shade and organic substrate of the forest floor (Knapp & Smith 1982), but spruce has greater longevity. Engelmann spruce commonly lives beyond 500 years, whereas subalpine fir ages rarely exceed 300 years (Oosting & Reed 1952; Fowells 1965; Day 1972; Veblen 1986a, b). Different interpretations of these life-history traits have led to characterizations of spruce–fir forests as both successional and climax communities (Peet 1981b, in press; Aplet, Laven & Smith 1988).

Sampling and analysis

Nine stands of differing age since initiation were selected to represent a chronosequence of stand development in Colorado spruce–fir forests (Table 1). Stand age was considered to be the age of the oldest trees in the oldest post-disturbance cohort in the stand. As stands approach or exceed the life expectancy of Engelmann spruce, stand age becomes more difficult to determine. However, even-aged remnants of the colonizing cohort are apparent in all but Stand 9. Stands were restricted generally to northern aspects, although aspect ranged from east to north-west. To minimize the effect of a third species, none of the chosen stands had more than 5% lodgepole pine stems.

Three 0.1 or 0.05-ha plots were established in eight of the nine selected stands. Stand 1 was sampled using eight 0.01-ha plots. Species, diameter at breast height (dbh) and bark thickness were recorded for living trees > 5 -cm dbh. A subsample of about 33% of the trees in each stand was cored for age determination, and age-class distributions were constructed according to the methods described in Aplet, Laven & Smith (1988). Additionally, a subsample of two trees of each species from each 5-cm dbh class was measured for height, and local height-diameter relationships were derived. Estimated height and dbh were then used to calculate stemwood volume using the equations of Myers & Edminster (1972). Stemwood volume was converted to stemwood biomass using densities of 368 and 433 kg m⁻³ air dry wt for spruce and fir (Wenger 1984).

In addition, each tree was cored at breast height for radial growth increment. Ten-year radial growth was subtracted from the radius of each tree and a new volume was calculated without adjusting for height growth. Ten-year stemwood volume increment was converted to annual stemwood biomass increment and used as the estimate of production. Net production was not adjusted for loss to mortality during the 10-year period.

The breast-height cores were also marked in the field for sapwood length. The cross-sectional area of sapwood was calculated, and the amount of foliage area per tree (all-sided) was estimated using the regression equations of Kauffman & Troendle (1981). From these data, leaf area index (LAI), the amount of foliage area per unit of ground area occupied, was determined. Where two stands of the same age were sampled, data were averaged to produce single values for each stand age. Biomass, production and leaf area data were combined for Stands 3 and 4, Stands 5 and 6, and Stands 7 and 8.

In utilizing a chronosequence, vegetation change is inferred by assuming that the only difference between study plots is time and that the constructed chronology represents the vegetation change that would occur on one plot over time. Inherent in this approach is the assumption that all variation that influences the kinds and rates of vegetation change will be relatively uniform from one plot to the next during the course of stand development (Laven 1982). In spite of restricting slope, aspect, parent material and climate in this study, other unknown plot-to-plot variation (e.g. initial density and species composition, site quality, stand history) may exist. Therefore, the results of our chronosequence should be interpreted with caution and limited to the specific study area.

RESULTS

Size-class distributions at different stages of stand development differed markedly between species (Fig. 1). Spruce size-class distributions had a generally decreasing monotonic form early in stand development (Stands 1 and 2) but became unimodal after about 250 years (Stands 3, 4, 6, 7 and 9). In some stands (Stands 5 and 8), a bimodal distribution has recently developed. In contrast, fir size-class distributions maintained a decreasing monotonic form throughout stand development (Fig. 1).

Age-class structures (Aplet, Laven & Smith 1988) explain much of the variability in size-class structure. In the youngest stands, spruce > 5 -cm dbh range in age from 75 to 175 years. Under intense competition at high densities, a decreasing monotonic size distribution will form even in closely even-aged populations (Harper 1977). With further stand development, the smallest trees die, and the size distribution becomes unimodal. In Stands 3, 4, 6, 7 and 9 there has been no significant recruitment of spruce into the > 5 -cm dbh stratum for at least 200 years (Table 1) and, as a result, the unimodal

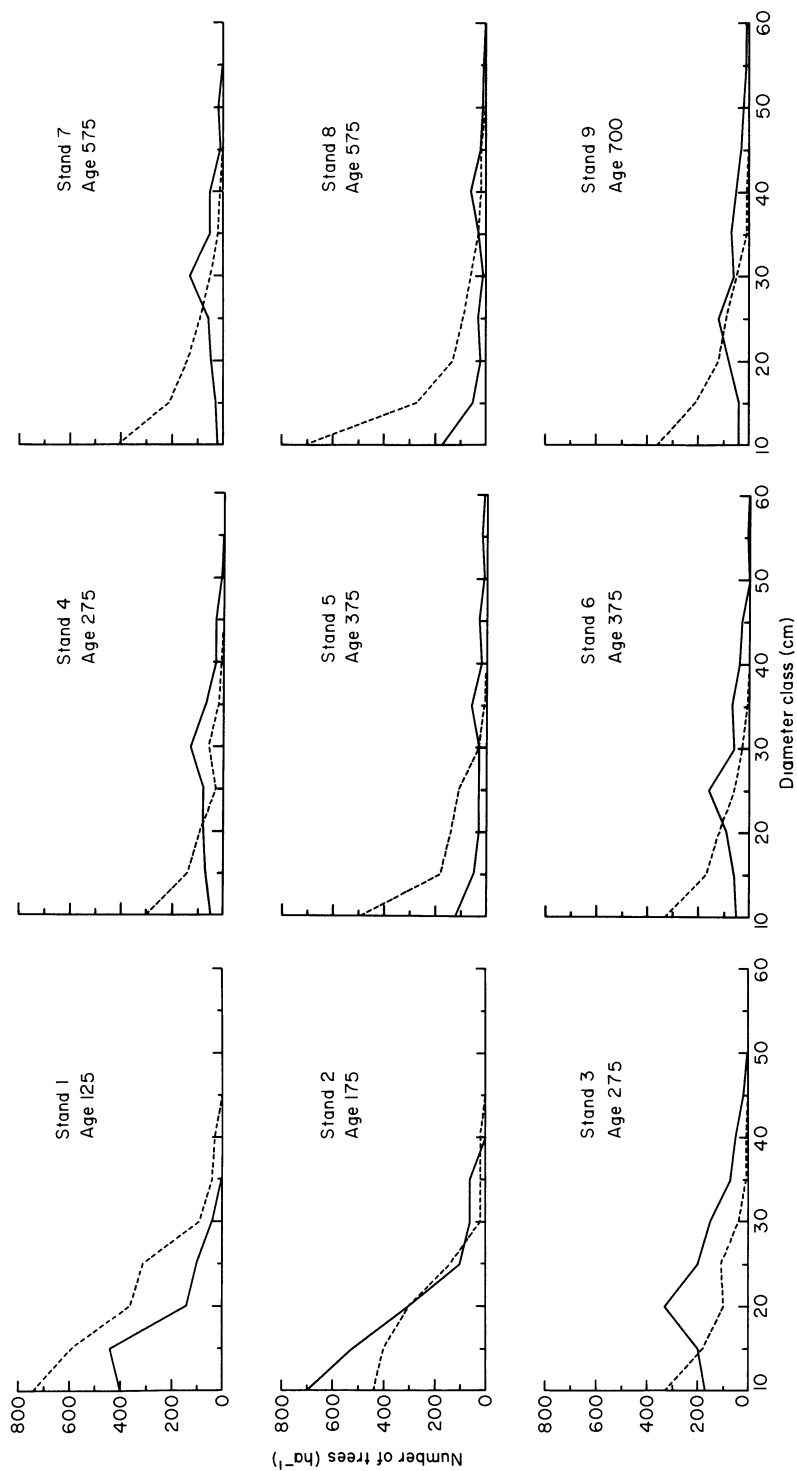


FIG. 1. Size-class distributions of spruce (—) and fir (---) from nine stands in north-central Colorado. Sizes are grouped into 5-cm dbh classes. Trees < 5-cm dbh were not included.

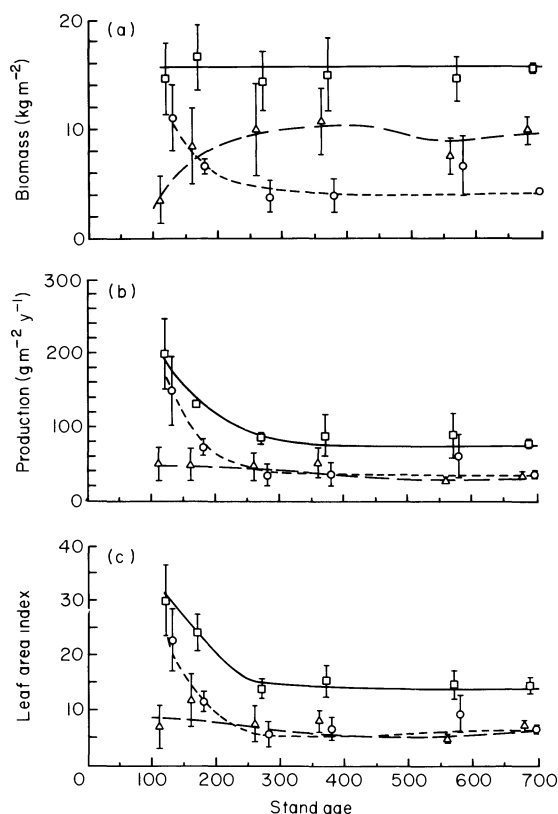


FIG. 2. Levels of spruce (\triangle), fir (\circ) and total (combined) (\square) live stemwood biomass (a), stemwood production (b) and leaf area index (all-sided) (c) in nine stands in north-central Colorado. Stands of similar age have been combined (see text). Error bars represent one standard deviation from the mean at each stand age.

shape is retained. Only in Stands 5 and 8 have many spruce recently grown into the $> 5\text{-cm}$ dbh class, resulting in a bimodal size-class distribution.

Fir recruitment into the $> 5\text{-cm}$ dbh class has been continuous in all stands. Abundant saplings < 75 years old are too small to be included in the size distributions (except for Stand 8), but regular growth into larger classes ensures the persistence of the decreasing monotonic form.

Total stemwood biomass was nearly constant over the entire range of stand ages (Fig. 2a). Stand values varied between 12.7 and 17.5 kg m^{-2} and averaged 15.0 kg m^{-2} , but the proportion of the total contributed by each species changed markedly over stand development. At 125 years, only 25% of the total stemwood biomass was spruce. By age 175, spruce contributed 51% of the total and averaged 64% of the total over the remaining 500 years of stand development. In contrast, maximum fir stemwood biomass (11.0 kg m^{-2}) occurred in the youngest stand at age 125. Fir stemwood biomass decreased to 6.6 kg m^{-2} by age 175, and averaged 5.0 kg m^{-2} in older stands.

Stemwood production was highest early in stand development but decreased to a constant level by age 275 (Fig. 2b). At age 125, total annual stemwood increment was

199 g m⁻² year⁻¹. By age 175, production decreased to 131 g m⁻² year⁻¹, and averaged only 88 g m⁻² year⁻¹ in stands over 200 years old. Spruce production was relatively constant throughout stand development. Values ranged between 26 and 69 g m⁻² year⁻¹ and averaged 44 g m⁻² year⁻¹ over the range of ages sampled. In contrast, maximum fir production (149 g m⁻² year⁻¹) occurred at age 125 and decreased to a relatively constant level after 200 years of stand development. Fir production in six of the seven stands over age 200 ranged between 27 and 48 g m⁻² year⁻¹. Only Stand 8 exceeded this range with a biomass increment of 83 g m⁻² year⁻¹.

Changes in LAI relative to stand age were similar to changes in production (Fig. 2c). Total stand LAI was highest at age 125 with a LAI of 30.4 and decreased to 24.6 by age 175. Stands over 200 years old maintained a relatively constant LAI, averaging 15.1 for the seven oldest stands. Spruce LAI was relatively constant over the range of ages sampled. The highest value (12.1) occurred at age 175, the lowest in 575 year old Stand 8 (4.5), and spruce LAI averaged 7.8 for the nine stands. In contrast, maximum fir LAI exceeded 23.1 at age 112 but was only 5.7 in Stand 3 at age 275. The average fir LAI of stands over 200 years old (7.6) was similar to that of spruce.

Because 10-year growth and sapwood length were obtained from the same core, we examined sapwood rings to determine if radial increment and sapwood length were correlated. If sapwood length were highly correlated with radial increment, there would be a species-specific number of annual rings in the sapwood. The number of sapwood rings ranged from 15 to 56 for fir (\bar{x} = 26.1, S.E. = 10.3, n = 33) and from 12 to 135 for spruce (\bar{x} = 63.5, S.E. = 29.6, n = 26). Thus, sapwood length does not translate directly into radial increment; a relationship between sapwood area and volume increment would not be a consequence of the method of measurement.

DISCUSSION

Nearly constant values of total stemwood biomass (Fig. 2a) suggest that Engelmann spruce-subalpine fir forests maintain equilibrium biomass levels for several hundred years of stand development. Low mortality rates early in stand development (Aplet, Laven & Smith 1988) suggest that the equilibrium value is also the maximum value. Thus, total stemwood biomass appears to behave according to Peet's first model; biomass rises asymptotically to a maximum level and is maintained through ensuing stand development.

Total stemwood production, in contrast, reaches its maximum value early in stand development before decreasing to an asymptotic level (Fig. 2b). Whether or not this maximum occurs before age 125 years, or is significantly higher than that observed at 125 years remains unresolved.

Rather than being intrinsic to communities, these patterns result from the interactions of specific behaviours of two populations. Early in stand development, total biomass is dominated by fir but shifts with time to dominance by spruce (Fig. 2a). Stemwood production shifts from being strongly affected by fir production to a level equally affected by both species (Fig. 2b). These changes arise from differences in the timing of population processes during community development (Aplet, Laven & Smith 1988). Following disturbance which destroys a stand, both spruce and fir establish and occupy the denuded site. As development proceeds and density increases, spruce recruitment slows or halts, but fir recruitment continues. During this period, fir biomass and production reach their maximum levels. By the third century, however, the oldest, largest fir trees, which

originally colonized the site, begin to die. The largest fir trees are lost from the stand, and the fir diameter distribution assumes a characteristic inverse-J shape. Fir biomass and production levels both decrease to equilibrium levels.

Spruce population development proceeds differently. Reduced spruce regeneration and mortality in the smallest stems leads to a transformation of diameter-class structure from a decreasing monotonic form to a unimodal form by the third century (Fig. 1, Stands 3 and 4). Mortality in the fir component may stimulate the establishment of spruce in the understorey, and continued establishment and growth eventually lead to a bimodal diameter-class structure (Fig. 1, Stands 5 and 8). Despite these changes in structure, spruce biomass and production remain relatively constant after 200 years.

Species' biomass and production early in stand development may be strongly influenced by initial conditions. The high levels of fir biomass and production in the youngest stand may reflect a high initial density of fir in this stand. Stands on very different sites or with a different initial species composition could perform differently.

As would be expected in a community composed of such ecologically similar species, the two populations are not independent. Mortality in the fir component early in stand development allows the establishment of spruce in the understorey. Similarly, death of large spruce late in stand development may increase resource availability to fir, and increase production and biomass levels. Interspecific competition must also limit the rate of accumulation and amount of standing biomass of each species. Despite the population interactions, biomass and production levels of both species remain remarkably stable over much of stand development.

The disparate population behaviours observed in this study appear to be best explained by changes in leaf area. Changes in fir, spruce and total production closely track changes in respective leaf areas. Total and fir LAIs rise early in stand development to values above the sustainable level (Fig. 2c). High leaf areas for young stands have been reported in many even-aged forests immediately preceding a period of increased mortality (Waring & Schlesinger 1985). This appears to occur in the fir component of the study area forests as well, despite its all-aged structure. Maximum fir biomass, productivity and LAI all occur before the period of mortality in the fir component. With the loss of the old, large firs from the diameter-class structure, some LAI and associated production are lost from the stand. The stable size-class structure exhibited throughout ensuing stand development fixes fir LAI and production at a reduced, equilibrium level.

The relation between spruce size-class structure and LAI is much different. Like production, spruce LAI is relatively constant despite the relatively even-aged structure of some stands. Concurrent changes in diameter-class structure imply that LAI is continually being re-allocated to fewer, larger trees and then to smaller, younger trees as spruce reinitiation occurs. This constant level of leaf area appears to control spruce production as well.

Fir and spruce stemwood production is directly related to leaf area in these stands. However, equilibrium leaf area occurs under different population structures in the two species. Equilibrium leaf area for fir is achieved and maintained in conjunction with a stable size-class structure. Equilibrium leaf area for spruce is achieved and maintained despite substantial changes in size-class structure.

Variation in biomass and production dynamics may be due to the various behaviours of individual species in mixed-species communities. In the forests studied here, total biomass rises asymptotically despite different behaviours in the component species. Subalpine fir appears to follow Peet's second model, while Engelmann spruce may behave according to

the first model or as a long-period, oscillating species. A monospecific community of either species would behave quite differently from the current mixture. Similarly, another multispecies community, comprising species with alternative behaviours, may not develop as the community described here.

ACKNOWLEDGMENT

This research was supported by a McIntire-Stennis grant.

REFERENCES

- Aplet, G. H., Laven, R. D. & Smith, F. W. (1988). Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. *Ecology*, **69**, 312–319.
- Day, R. J. (1972). Stand structure, succession, and use of southern Alberta's Rocky Mountain forest. *Ecology*, **53**, 472–478.
- Fowells, H. A. (1965). *Silvics of Forest Trees of the United States*. U.S. Department of Agriculture, Agriculture Handbook 271.
- Harper, J. L. (1977). *The Population Biology of Plants*. Academic Press, London.
- Horn, H. S. (1971). *The Adaptive Geometry of Trees*. Princeton University Press, Princeton, New Jersey.
- Horn, H. S. (1974). The ecology of secondary succession. *Annual Review of Ecology and Systematics*, **5**, 25–37.
- Kauffman, M. R. & Troendle, C. A. (1981). The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. *Forest Science*, **27**, 477–482.
- Knapp, A. K. & Smith, W. K. (1982). Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. *Canadian Journal of Botany*, **60**, 2753–2761.
- Laven, R. D. (1982). Establishing homogeneity in studies of forest succession. *Forest Ecology and Management*, **4**, 161–177.
- Margalef, R. (1963). On certain unifying principles in ecology. *American Naturalist*, **97**, 357–374.
- Myers, C. A. & Edminster, C. B. (1972). *Volume tables and point-sampling factors for Engelmann spruce in Colorado and Wyoming*. USDA Forest Service Research Paper, RM-95, 1–23. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Odum, E. P. (1969). The strategy of ecosystem development. *Science*, **164**, 262–270.
- Oosting, H. J. & Reed, J. F. 1952. Virgin spruce-fir of the Medicine Bow Mountains, Wyoming. *Ecological Monographs*, **22**, 69–91.
- Peet, R. K. (1981a). Changes in biomass and production during secondary forest succession. *Forest Succession: Concepts and Application* (Ed by D. C. West, H. H. Shugart & D. B. Botkin), pp. 324–338. Springer-Verlag, New York.
- Peet, R. K. (1981b). forest vegetation of the Colorado Front Range: composition and dynamics. *Vegetatio*, **45**, 3–75.
- Peet, R. K. (in press). Forests of the Rocky Mountains. *North American Terrestrial Vegetation* (Ed by M. G. Barbour & W. D. Billings), pp. 64–101. Cambridge University Press, New York.
- Veblen, T. T. (1986a). Treefalls and coexistence of conifers in subalpine forests of the central Rockies. *Ecology*, **67**, 644–649.
- Veblen, T. T. (1986b). Age and size structure of subalpine forests in the Colorado Front Range. *Bulletin of the Torrey Botanical Club*, **113**, 225–240.
- Vitousek, P. M. & Reinert, W. A. (1975). Ecosystem succession and nutrient retention: a hypothesis. *Bioscience*, **25**, 376–381.
- Waring, R. H. & Schlesinger, W. H. (1985). *Forest Ecosystems: Concepts and Management*. Academic Press, New York.
- Wenger, K. F. (1984). *Forestry Handbook*. John Wiley & Sons, New York.

(Received 5 October 1987; revision received 15 April 1988)